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GRASSLAND SONGBIRDS IN A DYNAMIC MANAGEMENT LANDSCAPE: BEHAVIORAL RESPONSES AND MANAGEMENT STRATEGIES

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Abstract. In recent decades, earlier and more frequent harvests of agricultural grasslands have been implicated as a major cause of population declines in grassland songbirds. From 2002 to 2005, in the Champlain Valley of Vermont and New York, USA, we studied the reproductive success of Savannah Sparrows (*Passerculus sandwichensis*) and Bobolinks (*Dolichonyx oryzivorus*) on four grassland treatments: (1) early-hayed fields cut before 11 June and again in early- to mid-July; (2) middle-hayed fields cut once between 21 June and 10 July; (3) late-hayed fields cut after 1 August; and (4) rotationally grazed pastures. Both the number of fledglings per female per year and nest success (logistic-exposure method) varied among treatments and between species. Although birds initiated nests earlier on early-hayed fields compared to others, haying caused 99% of active Savannah Sparrow and 100% of active Bobolink nests to fail. Both the initial cutting date and time between cuttings influenced re-nesting behavior. After haying, Savannah Sparrows generally remained on early-hayed fields and immediately re-nested (clutch completion 15.6 ± 1.28 days post-haying; all values are reported as mean \pm SE), while Bobolinks abandoned the fields for at least two weeks (mean clutch completion 33 ± 0.82 days post-haying). While female Savannah Sparrows fledged more offspring per year (1.28 ± 0.16) than female Bobolinks (0.05 ± 0.05), reproductive success on early-hayed fields was low. The number of fledglings per female per year was greater on middle-hayed fields (Savannah Sparrows, 3.47 ± 0.42 ; Bobolinks, 2.22 ± 0.26), and late-hayed fields (Savannah Sparrows, 3.29 ± 0.30 ; Bobolinks, 2.79 ± 0.18). Reproductive success was moderate on rotationally grazed pastures, where female Savannah Sparrows and female Bobolinks produced 2.32 ± 0.25 and 1.79 ± 0.33 fledgling per year, respectively.

We simultaneously conducted cutting surveys throughout the Champlain Valley and found that 3–8% of hayfield habitat was cut by 1–4 June, 25–40% by 12–16 June, and 32–60% by 28 June–2 July. Thus, the majority of grassland habitat was cut during the breeding season; however, late-hayed fields served as high-quality reserves for late-nesting female Bobolinks that were displaced from previously hayed fields. For fields first cut in May, a 65-day interval between cuts could provide enough time for both species to successfully fledge young.

Key words: Bobolink; *Dolichonyx oryzivorus*; fledglings per year; grassland management; hayfield; logistic exposure; nest success; New York; *Passerculus sandwichensis*; rotationally grazed pasture; Savannah Sparrow; Vermont.

INTRODUCTION

North American grassland songbird population declines from the 1960s to the present are strongly associated with changes in agricultural land use (Bollinger and Gavin 1992, Sampson and Knopf 1994, Warner 1994, Herkert 1997, Askins 1999, Peterjohn and Sauer 1999, Warren 2005). This trend is especially apparent in the northeastern United States, where grassland songbird populations have declined rapidly.

From 1966 to 1994, 14 of 19 grassland and savannah bird species significantly declined in northeastern North America (Askins 1999), and recent surveys indicate low species diversity (Shustack 2004).

The process of grassland management in the Northeast has changed in recent decades, with earlier first harvest dates and more frequent harvests (Bollinger et al. 1990, Troy et al. 2005). Since the 1960s, hay farmers have advanced the initial cutting date from mid-summer to late May or early June because forage protein levels are higher early in the growing season (Cherney et al. 1993), which in turn increases the milk production by lactating dairy cows (Bosworth and Stringer 1985). The effects of these changes are critical because in the

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Northeast, hayfields and pastures serve as the primary breeding habitat for obligate grassland songbirds (Bollinger and Gavin 1992, Shustack 2004).

Early hayfield management occurs at a vulnerable time in the breeding cycle of grassland songbirds. In early- to mid-June most birds are in the late incubation stage or have young nestlings. Since most grassland birds nest on the ground, the eggs and nestlings are vulnerable to being crushed by the harvest machinery. Although some intact nests may survive the harvest process, nest failure can also occur by abandonment or post-haying predation, as avian predators and small mammals often search recently hayed fields, preying on exposed eggs, nestlings, and fledglings (Bollinger et al. 1990). Additionally, greater harvesting frequency results in a shorter window of opportunity (35 days) to renest between haying events. For many grassland birds, the nesting cycle, including nest building, egg laying, incubation, and nestling feeding, lasts ~28 days. When fledging occurs, however, nestlings walk out of the nest and cannot fly. Therefore, young fledglings are also vulnerable to haying events. In terms of timing and cutting intervals, hayfield management is a clear threat to grassland nesting songbirds.

Modernized hayfield management has a strong negative effect on songbird demography, though only a few studies have examined this relationship. Both Nocera et al. (2005) and Dale et al. (1997) used point-count data to determine whether delayed hay dates positively affected breeding songbirds. Only Warner and Etter (1989) and Bollinger et al. (1990) measured individual female demography relative to the types of management-defined grassland habitats they select. Their studies documented, however, only the immediate nest destruction of haying and did not consider whether the timing of management may impact species differently over the course of the nesting season.

Though these studies clearly demonstrated that haying causes high nest, nestling, and fledgling mortality, whether songbird demography varies under a diversity of haying regimes remains unclear. As a result, recommendations to increase songbird productivity in grassland-based agricultural landscapes have unanimously focused on the value of delaying hay harvest to mid-July or August (Bollinger and Gavin 1992, Nocera et al. 2005, Warren and Anderson 2005). Nonetheless, in agricultural regions, due to financial and nutritional needs, delaying initial hay harvest is not an option for most farmers (Troy et al. 2005). Therefore, in working landscapes, grassland management plans that balance both farmers' and birds' needs are critical for long-term conservation planning. Northeastern grassland landscapes and the populations they support are dynamic over time and space (Norment 2002). To understand the effects of grassland management on a larger breeding population, we need detailed demographic data that describe how multiple species of songbirds behave within diverse management scenarios

that are representative of the agricultural landscape. Additionally, we need to gather information within a larger system about how hayfields are managed within and between seasons.

To address these questions, we initiated a demographic study of two obligate grassland songbirds breeding in agricultural grasslands within the Champlain Valley of Vermont, USA and New York, USA. Our objectives were (1) to describe Bobolink (*Dolichonyx oryzivorus*) and Savannah Sparrow (*Passerculus sandwichensis*) nesting phenology and breeding behavior relative to four management-defined grassland treatments; (2) to determine if nest success and nest survival differed among the four grassland treatment types; (3) to evaluate the effect of delayed first harvest on nest success and the number of fledglings produced per female per year; (4) to describe how hayfields are managed both within a year and between consecutive years throughout the Champlain Valley; (5) and to describe management scenarios that can provide high quality grassland songbird breeding habitat in the Champlain Valley.

METHODS

Study area

Research took place from May to August 2002–2005 in the Champlain Valley, a relatively isolated system bordered by Vermont's Green Mountains on the east and New York's Adirondack Mountains on the west. As the main dairy land for Vermont and eastern New York, the Valley includes 146 000 ha of mostly privately-owned managed grasslands (NASS 1999). Roughly 65% of these grasslands are managed as forage fields for dairy and beef cows.

Bobolinks and Savannah Sparrows account for the majority (72%) of the Champlain Valley's grassland nesting bird community (Shustack 2004). Other species nesting in low densities within the valley's grasslands include the Eastern Meadowlark (*Sturnella magna*), Red-winged Blackbird (*Agelaius phoeniceus*), Grasshopper Sparrow (*Ammodramus saviarum*), Upland Sandpiper (*Bartramia longicauda*), Northern Harrier (*Circus cyaneus*), and Horned Lark (*Eremophila alpestris*).

Study species

Bobolink and Savannah Sparrow life history strategies have both similarities and differences, which make them an ideal pair to examine how management affects a community of grassland songbirds. On the breeding grounds, the two species have similar patterns of resource use. Both species are grassland obligates that feed on insects, use dried grass to build nests on the ground, and have nesting cycles lasting 23–25 days. However, differences in migration and wintering location influence breeding strategies. Savannah Sparrows are short-distance migrants (Wheelwright and Rising 1993), arriving on the Champlain Valley breeding grounds in mid- to late April. Nesting spans from early

May to mid-August, which allows them enough time to attempt two broods (Wheelwright et al. 1992). In contrast, Bobolinks are long-distance migrants (Martin and Gavin 1995), arriving on their Champlain Valley breeding grounds in mid-May. Breeding occurs from late May to mid-July. This brief window generally provides enough time to raise only one brood, although Bobolinks will occasionally reneest after early failure (Martin 1971, Gavin 1984).

Experimental design

To assess the impacts of grassland management on the population ecology of Bobolinks and Savannah Sparrows, we studied the four major grassland treatment types in the Champlain Valley: (1) *Early-hayed fields* (EH), hayed between 27 May and 11 June and generally again in early- to mid-July; (2) *Middle-hayed fields* (MH), hayed between 21 June and 10 July; (3) *Late-hayed fields* (LH), hayed after 1 August; (4) *Rotationally grazed pastures* (RG), fields in which cows were rotated through a matrix of paddocks and moved after all of the grass in a paddock was eaten to a farm-specific height so that vegetation in each paddock was given a multiple-week "rest" between grazing events.

We established treatment fields in three study areas: (1) Shelburne, Vermont (2002–2005) (EH, LM, RG), (2) Hinesburg, Vermont (2003–2005) (EH, LH, MH, RG), and (3) Cumberland Head, New York (2002–2004) (MH, LH). We interviewed landowners and managers to identify fields whose long-term management fell into our treatment definitions. We then selected fields based on size (large enough to include a 10.5-ha focal study plot; field size ranged from 13.2 to 38.3 ha; mean = 21.1 ha), and proximity (>8 km) to other study areas. Land use within each study area was consistent for at least 10 years prior to the initiation of our study. Fields were composed of a mixture of cool season grasses and forbs. Early- and middle-hayed fields had greater forb composition than late-hayed fields or pastures, including alfalfa (*Medicago sativa* L.), red clover (*Trifolium pratense* L.), white clover (*Trifolium repens* L.), and dandelion (*Taraxacum officinale* Weber). Late-hayed fields and rotationally grazed pastures were grass dominated, including orchard grass (*Dactylis glomerata* L.), timothy, (*Phleum pratense* L.), and bluegrass (*Poa* sp.), and reed canarygrass (*Phalaris arundinacea* L.). However, late-hayed fields generally had significant "old-field" communities, including sedge (*Carex* spp.), vetch (*Vicia* sp.), bedstraw (*Galium* sp.), and native forbs.

The two replicates of rotationally grazed pasture were stocked with heifers and dry cows at a ratio of 1–1.5 cow/0.4 ha. The Hinesburg pasture was in management-intensive grazing (MIG) practice, where the paddock was grazed to 5–10 cm, and the cows were rotated every seven days. The Shelburne pasture was in a light grazing rotation, where grass was grazed to 10–20 cm, and cows were rotated every 7–14 days. All early- and middle-hayed fields were cut with disc mowers that left 5–10 cm

grass stubble. After these fields were cut, the grass was treated with either a rake or conditioner, and then round-baled or chopped. In most years, liquid manure was spread on early-hayed fields 2–10 days after the first cut. Late-hayed fields were cut both with disc mowers and brush hogs (12–18 cm), and in some years the grass was left on the field in wide windrows.

Field methods

Beginning in early May, we captured territorial birds with mist-nets, and put unique combinations of three color bands and a single metal U.S. Fish and Wildlife Service band on the legs of all adults of both species. Color-banded birds were continuously resighted throughout the breeding season. In mid-May we began intensive, season-long nest searching and nest monitoring to assess annual fecundity. Although we did not make rigorous density estimates on the fields, our impression was that densities were relatively consistent among treatments, with the exception of rotationally grazed fields, which had lower densities of Bobolinks. We attempted to find nests of all females that bred on each treatment field. We located nests by observing adult behavior and by flushing incubating females off their nests while walking through the fields swishing bamboo sticks. The majority of nests were found during the incubation stage (64.9%); the rest were found during the nest building (1.8%), egg laying (15.1%), hatching (3.6%), and nestling stages (14.6%). After locating a nest, we immediately identified the associated female and male. If one or both adults were unbanded, we captured those individuals near the nest location. Females could typically be assigned to nests unambiguously through incubation and brooding behavior. We determined male nest association by observing territory defense, mate guarding, and food deliveries (Wheelwright and Rising 1993, Martin and Gavin 1995).

Each nest was marked with a single bamboo stake and colored flagging placed 2–5 m from the nest. While nest markers can slightly increase avian predation of passerine nests (Gotmark 1992), we took care to minimize these effects by both setting random stakes throughout fields and by posting a 50 × 50 m grid throughout each field. We visited nests every one to two days until fledging or failure. Nestlings were weighed and banded with a single metal U.S. Fish and Wildlife Service band on day six or seven. A nest was considered successful if at least one bird fledged.

On early- and middle-hayed fields, we monitored nests immediately before and after the nest area was hayed. Ring-billed Gulls (*Larus delawarensis*), Common Ravens (*Corvus corax*), and American Crows (*Covus brachyrhynchos*) followed the haying machinery and preyed upon revealed nests, fledglings, insects, mammals, and amphibians. We did not disturb the predators' foraging efforts. Behavioral observations of adults caring for known-age fledglings and subsequent reneesting patterns showed that young fledglings did not

survive haying events. While we believe that juveniles seven days post-fledgling may not survive haying events, this study was not designed to precisely evaluate fledgling survival. However, in the absence of fledgling survival data, we conservatively considered nestlings that left a given nest within three days prior to a haying event as a failed nest. We measured annual nesting phenology and breeding behavior by following the maximum number of females available on each field throughout the reproductive year for as long as they remained on the respective field. We quantified the number of offspring produced in a breeding season by each adult female.

Analysis methods

Nesting phenology and breeding demographics.—Nesting phenology was evaluated with both clutch completion and fledging dates. Clutch completion dates illustrated both spring settlement patterns as well as re-nesting patterns. Nest contents that survived either from egg-laying to incubation, incubation to hatching, or nestling to fledging, were included in the phenology analysis. For such eggs or chicks, we obtained clutch completion dates by back-calculating from either the hatching or fledging date. We used all nests to analyze breeding demographics (number of offspring produced per female per year, clutch size, number of clutches per female) among treatments and between species with two-way ANOVA tests in PROC MIXED (SAS Institute, Cary, North Carolina, USA).

Nest success and daily nest survival.—We used the logistic-exposure method (hereafter, L-E; Shaffer 2004) to model nest success and daily nest survival. The L-E model is a likelihood-based modeling approach that allows unbiased estimation of daily nest survival and inclusion of covariates that may influence daily nest survival. Rather than treating each nest as a sample, the number of days between nest checks (an interval) is the primary focus. The model uses a binomial framework to estimate the probability that a nest will survive (or fail) through the interval. Given a large number of intervals, the number of days within each interval, and a specified model, the analysis finds the most likely daily survival estimates. Various competing models are then ranked and compared using an information theoretic approach. The L-E method is a powerful analytical tool for data sets with variable intervals between observations because nest-check intervals are weighted by the interval length. This method assumes that the fate of all nests is independent of other nests, and that daily survival probabilities are both homogenous across the nest cycle and are affected similarly by explanatory variables (Shaffer 2004). Early-hayed, middle-hayed, and grazing within this study all directly affect nest success and therefore bias the assumption of independence. However, the effects of predation and weather, both significant causes of nest failure, were independent. While most nest-check intervals were between one and two days,

nests subjected to management (haying) were monitored just prior to haying and immediately after haying, intervals as short as 10 minutes. In order to use the information gathered from these precise visits, our L-E modeling occurred at hourly intervals later scaled up to daily intervals for nest survival estimates. While shorter intervals may increase observer-caused nest failure, the precise information gained from these observations was critical to the research objectives.

We used an information-theoretic approach (Burnham and Anderson 2002) to compare alternative nest-success models. Our a priori model set was developed from the data reported by Bollinger et al. (1990) and Bollinger and Gavin (1992). Their study found that hayfield management caused >90% of active Bobolink nests to fail. However, because weather is a major determinant of when farmers begin haying in the Champlain Valley, we included year in the variable set to examine how treatment stochasticity affected nest success. Finally, because Bobolinks and Savannah Sparrows have distinct breeding strategies but are equally subject to both haying and annual stochasticity, we included species in model sets. Therefore, our 10 individual, additive, and interaction models examine how grassland treatment type ($n=4$), species ($n=2$), and year ($n=4$) affected nest success. The nest-success models were species only; year only; treatment only; year + species; treatment + year; treatment + species; treatment + species + year; treatment \times species interaction; year \times species interaction; treatment \times year interaction. All statistical analyses were performed with SAS 8.0.

Daily nest survival was determined as $\text{DNS} = \exp(\log\text{-odds}) / [1 + \exp(\log\text{-odds})]$, where the model-specific logit followed the linear equation:

$$\begin{aligned} \log\text{-odds}(\text{DNS}) = & \text{intercept} + \beta_1(X_1) + \beta_2(X_2) + \beta_3(X_3) \\ & + \dots + \beta_X(X_X) \end{aligned}$$

and X_i were the covariate values associated with the nest or the nest interval, and β_i was the corresponding effect size. Nest success was calculated as the daily nest survival raised to the exponent of the nest cycle length and included the egg laying, incubation, and nestling stage. Nest cycles were 23 d for Savannah Sparrows and 25 d for Bobolinks. Models that did not include species as a parameter were scaled to an average 24-d nesting period. We used model averaging to obtain overall nest success values. Here, we summed the products of the daily nest survival against their AIC_c weight (ω_i) for the top six ranking models, which accounted for >99% of model AIC_c weights. The model-averaged 95% confidence intervals were calculated with the intercept (β_0) and coefficients (β_i) for the lower and upper estimates for each model.

Nest survival as a function of haying date.—We observed haying six times on early-hayed fields (27 and 28 May, and 3, 5, 7, and 11 June) and on middle-hayed

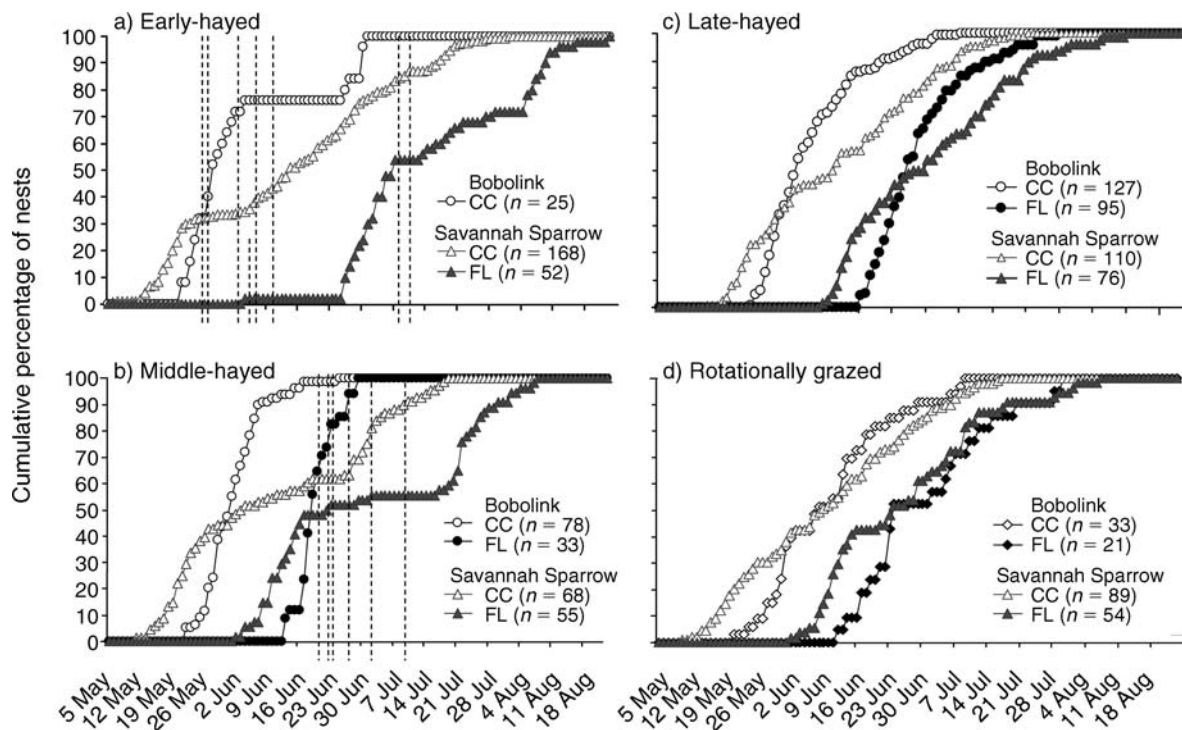


FIG. 1. Nesting phenology for Savannah Sparrows (*Passerculus sandwichensis*) and Bobolinks (*Dolichonyx oryzivorus*) in Champlain Valley (New York and Vermont) 2002–2005. Phenology was different between species and among treatments (a, early-hayed; b, middle-hayed; c, late-hayed; d, rotationally grazed pasture). Phenologies are presented on each field in terms of clutch completion dates (CC), indicating spring settlement and renesting behavior, as well as fledging (FL) phenology (where available). Sample sizes are in parentheses. Figures include all nesting attempts that survived at least one change of state, i.e., from egg-laying to incubation, incubation to hatching, or nestling to fledging. Vertical bars on early- and middle-hayed figures illustrate the observed haying events.

fields (21, 23, 24, and 27 June, and 2 and 10 July). The progressive nature of the haying dates granted an opportunity to model how nest success and nest survival varied as a function of the first haying date. Late-hayed fields were hayed after the nesting season, and were assigned a standardized haying date of 1 September. Renesting after a first cut was not included in this analysis because nest survival of the second nest was not directly affected by the first haying event.

Haying date was standardized with a Z transformation based on the mean (15 June) and standard deviation (14.3 days) of all haying dates across all years. Since nest fates were standardized across years, this analysis ignored year effects that may have influenced nest fate (predation, weather) and (log-odds) nest success was modeled as a function of haying date only. We performed a likelihood-ratio test to assess model fit by comparing this model to an intercept (null) model.

Cutting surveys.—To better understand the population level implications of our plot-based study, from late-May to mid-July we conducted cutting surveys on privately owned fields throughout the valley. These surveys assessed within-year and between-year patterns of grassland management. In 2002, 69 randomly selected hayfields (560 ha) (Shustack 2004) were visited every 10–

14 days to determine whether or not the field had been hayed. In 2003–2005, we expanded the survey to include the original 69 fields as well as all fields visible from the road survey point (increasing to between 278 and 355 fields and between 804 and 1019 ha, depending on the year).

RESULTS

Nesting phenology

Nesting phenology varied by treatment and species ($n = 576$ Savannah Sparrow nests; $n = 344$ Bobolink nests). On the early- and middle-hayed treatments, haying interrupted clutch completion and fledging for Savannah Sparrows (Fig. 1a, b) and Bobolinks (Fig. 1b). For Bobolinks on early-hayed fields (Fig. 1a), the timing of first nests (initial clutch completion through 6 June) and presumed re-nests of new immigrants settling post-haying (clutch completion dates 25 June–1 July) ensured that no nests successfully fledged young (with one exception, discussed later) before the second (early- to mid-July) haying. Early-haying resulted in substantial delays in fledging for Savannah Sparrows (Fig. 1a). With the exception of one nest that survived a first cut, Savannah Sparrows did not fledge young on early-hayed fields until after 26 June. On middle-hayed fields (Fig. 1b), no

TABLE 1. Fledglings produced per female per year, number of nests, and number of eggs laid by Savannah Sparrow (*Passerculus sandwichensis*) and Bobolink (*Dolichonyx oryzivorus*), by treatment type in the Champlain Valley (New York and Vermont) 2002–2005.

Parameter	Species	Treatment			
		Early-hayed field	Middle-hayed field	Late-hayed field	Grazed pasture
No. fledglings/female/year	Bobolink	0.05 (0.05)	2.22 (0.26)	2.79 (0.18)	1.79 (0.33)
	Savannah Sparrow	1.28 (0.16)	3.47 (0.42)	3.29 (0.30)	2.32 (0.25)
No. nests/year	Bobolink	1.00 (0.00)	1.03 (0.02)	1.05 (0.02)	1.09 (0.06)
	Savannah Sparrow	1.87 (0.10)	1.64 (0.08)	1.64 (0.08)	1.52 (0.08)
No. eggs/year	Bobolink	4.71 (0.18)	5.28 (0.13)	5.05 (0.11)	5.05 (0.29)
	Savannah Sparrow	7.35 (0.39)	6.44 (0.55)	6.58 (0.33)	5.73 (0.32)

Note: Standard errors are presented in parentheses.

Bobolinks renested after the haying period; thus, any successful nests fledged young prior (at least three days) to the first cut. By contrast, some Savannah Sparrows on middle-hayed fields fledged young prior to the cut (2–23 June), and some successfully renested or double-brooded after the cut (17 July–8 August). Patterns of clutch completion and fledging were similar within species between the late-hayed and pasture treatments, as both species fledged young throughout the breeding season (through 11 August for Savannah Sparrows and 28 July for Bobolinks; Fig. 1c, d). Savannah Sparrows showed greater within-season site fidelity after nest failure; thus, their extended nesting period was a result of both renesting and double brooding.

Both species showed significant differences in the timing of the first 18 clutch completion dates among treatments (one-way ANOVA; for Bobolinks, $F_{3,68} = 24.5$, $P < 0.01$; for Savannah Sparrows, $F_{3,68} = 14.98$, $P < 0.01$). We compared 18 nests because this is the maximum available on early-hayed fields for which to compare (subsequent nests failed due to haying). We discriminated between pairs of treatments within ANOVA models with least-square means tests (LSM). For Savannah Sparrows, mean clutch completion dates on early-hayed fields were significantly earlier than middle-hayed (LSM, $P < 0.01$), late-hayed (LSM, $P < 0.01$), and rotationally grazed pastures (LSM, $P < 0.01$). Middle-hayed fields were not significantly different than late-hayed (LSM, $P = 0.12$) or rotationally grazed pastures (LSM, $P = 0.55$). Mean clutch completion dates for late-hayed fields, however, were significantly earlier than pastures (LSM, $P = 0.03$). Analyses using first nests were similar to results obtained for mean nesting dates. Compared to late-hayed fields, Savannah Sparrow females began incubating nests nine days earlier on early-hayed fields, four days earlier on middle-hayed fields, and five days earlier on pastures. The earliest observed clutch completion date for Savannah Sparrows was 6 May and the latest was 30 July.

For Bobolinks, the first 18 clutch completion dates on early-hayed fields were significantly earlier than pastures (LSM, $P < 0.01$), while clutch completion dates on early- and late-hayed (LSM, $P = 0.54$) and early- and middle-hayed fields were not significantly different

(LSM, $P = 0.42$). Bobolink clutch completion dates were significantly earlier on middle-hayed fields than pastures (LSM, $P < 0.01$), and late-hayed fields were earlier than pastures (LSM, $P < 0.01$). As compared to late-hayed fields, Bobolinks began incubating three days earlier on early-hayed fields, two days earlier on middle-hayed fields, and three days later on pastures. For Bobolinks, the earliest observed clutch completion date was 21 May and the latest was 9 July.

To understand if renesting patterns varied among treatments, we examined how long it took female Savannah Sparrows to renest following failure of their first nest. In this analysis, haying caused all first nests to fail on early-hayed fields, while all first nests on the other three treatments failed for non-haying related causes. Renesting patterns were significantly different among treatments (one-way ANOVA, $F_{3,78} = 4.03$, $P = 0.01$). Least-square mean tests between paired treatments showed that renesting was significantly slower on early-hayed fields than on all other treatments (LSM, middle-hayed $P = 0.03$; late-hayed $P < 0.01$; grazed $P = 0.04$). Mean days to renest after failure were 15.6 ± 1.28 ($n = 48$) on early-hayed, 9.1 ± 0.83 ($n = 7$) on middle-hayed, 9.7 ± 1.3 ($n = 16$) on late-hayed fields, and 10.5 ± 0.90 ($n = 11$) on rotationally grazed pastures (all values reported are mean \pm SE). Interestingly, there is no significant difference in time to renest after a successful nest (one-way ANOVA, $F_{3,52} = 1.64$, $P = 0.19$). However, the mean number of days to renest was shorter on late-hayed fields (12.9 ± 1.57 , $n = 24$) as compared to early-hayed fields (18 ± 3.29 ; $n = 7$, LSM, $P = 0.12$), middle-hayed fields (17.6 ± 2.02 ; $n = 12$, LSM, $P = 0.90$), and pastures (16.8 ± 1.97 ; $n = 13$, LSM, $P = 0.74$).

Breeding demographics

Within a season, female Savannah Sparrows laid significantly more eggs than female Bobolinks in the same field (one-way ANOVA, $F_{1,482} = 24.10$, $P < 0.01$; Table 1). Mean number of eggs laid ($F_{3,280} = 2.14$, $P < 0.10$) and nests per year ($F_{3,281} = 1.58$, $P < 0.19$) were similar among treatments for Bobolinks, although the standard error was greatest on pastures, which suggested that these females had a greater tendency to renest

(Table 1). Bobolink clutches were significantly smaller on pastures as compared to all other treatments ($F_{3,294} = 4.17$, $P < 0.01$). Female Savannah Sparrows laid more eggs ($F_{3,326} = 3.81$, $P < 0.01$) and built more nests ($F_{3,326} = 3.28$, $P < 0.02$) in a season on early-hayed fields than other treatments. Females also laid more eggs on middle- than late-hayed fields (LSM, $P = 0.04$). Savannah Sparrow clutch size did not change significantly between nesting attempts on early-hayed fields ($F_{5,244} = 1.85$, $P = 0.10$) or pastures ($F_{3,107} = 1.58$, $P = 0.20$). Clutch size was significantly lower in late-hayed fields between the first and third attempts (LSM, $P < 0.01$) and decreased on middle-hayed fields between the second and third attempt (LSM, $P < 0.01$). Pooled among treatments, Bobolinks laid nearly one fewer egg in their second clutch than their first ($F_{2,295} = 5.01$, $P < 0.01$). These Bobolink data, however, should be interpreted with caution because only 5.4% of females ($n = 32$) renested on the same field within the same year (Fig. 2).

The number of offspring fledged per female per year was significantly different between species (one-way ANOVA, $F_{1,484} = 16.35$, $P < 0.01$, Table 1). Savannah Sparrow females fledged consistently more offspring than Bobolink females because they renested after failure and sometimes raised two broods. Female fledging rates were significantly different among treatments ($F_{3,614} = 29.74$, $P < 0.01$), although the interaction between species and treatment was not significant ($F_{3,484} = 0.68$, $P = 0.57$). On early-hayed fields, females of both species fledged fewer offspring than those on middle- (LSM, $P < 0.01$), late-hayed fields (LSM, $P < 0.01$), and pastures (LSM, $P \leq 0.01$). The number of fledglings produced per breeding season was similar between middle-hayed and late-hayed treatments for both species (LSM, $P \geq 0.43$; Table 1).

Causes of nest failure

Nests failed because of haying activities, cows, predation, weather, infertility, abandonment, and adult (female) mortality. As expected, certain categories of failure were associated with the fields' respective treatment types (Fig. 3). For example, on pastures, cows caused 39% of failures by either eating or trampling ($n = 38$) nests. Cows were more detrimental to Bobolinks (65% of failures; $n = 22$) than Savannah Sparrows (25% of failures; $n = 16$).

On early-hayed fields, 129 of the 130 (99.2%) active nests at the time of haying failed. Haying machinery directly caused 78% of these nests to fail. Predation caused failure of the remaining 22% of nests, mainly by Ring-billed Gulls, Common Ravens, and American Crows. Perhaps by chance, failure from predation was not an issue on middle-hayed fields, where predation caused only 1% of haying-related nest failure (99% of active nests were destroyed by machinery). We did not document or suspect any direct mortality of adults from haying machinery or predation.

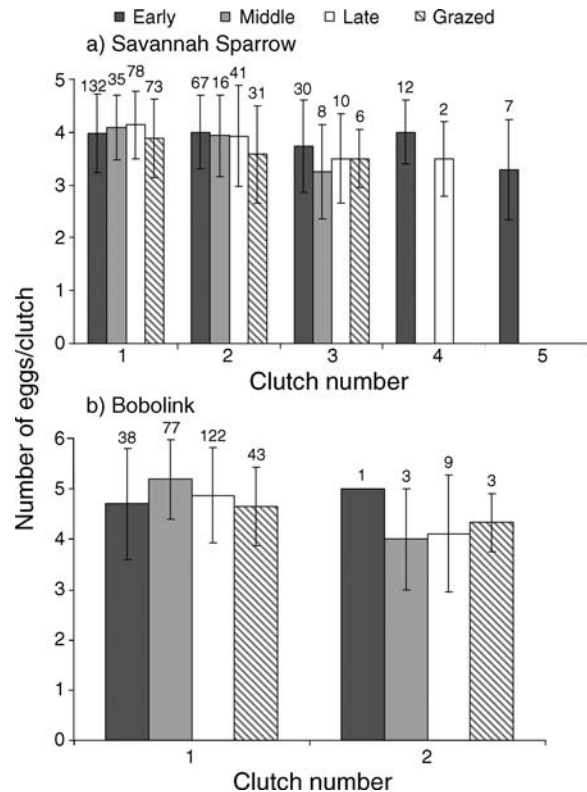


FIG. 2. The number of (a) Savannah Sparrow and (b) Bobolink eggs laid per clutch in the Champlain Valley (New York and Vermont) 2002–2005. Second Bobolink clutches had nearly one fewer egg, though samples were low because few marked females laid replacement clutches. Error bars indicate 95% confidence intervals, and numbers above each bar report sample size.

Despite similar productivity by birds nesting on late- and middle-hayed fields, the causes of failure between the two treatments differed. Predation caused 67% of all nest failures on late-hayed fields, but only 19% of nest failures on middle-hayed fields. On middle-hayed fields, haying activity accounted for 55% of failed nests.

Weather, mainly flooding, accounted for a large proportion of Bobolink failures on the late-hayed fields (27%) and Savannah Sparrow failures on the grazed pastures (30%). Only 1% of Savannah Sparrow nests and 2% of Bobolink nests on early- and middle-hayed fields failed from weather-related causes. This low proportion of weather related failures is notable, considering post-haying nests were generally more exposed due to low vegetative structure. While post-haying renews were exposed to heat and rain, they were more likely to fail due to predation.

Adult female mortality was extremely rare. We found three dead female Savannah Sparrows <1 m from their nests, but none showed any signs of injury. All cases of infertility were female Savannah Sparrows ($n = 2$) who laid multiple, infertile clutches within a given year.

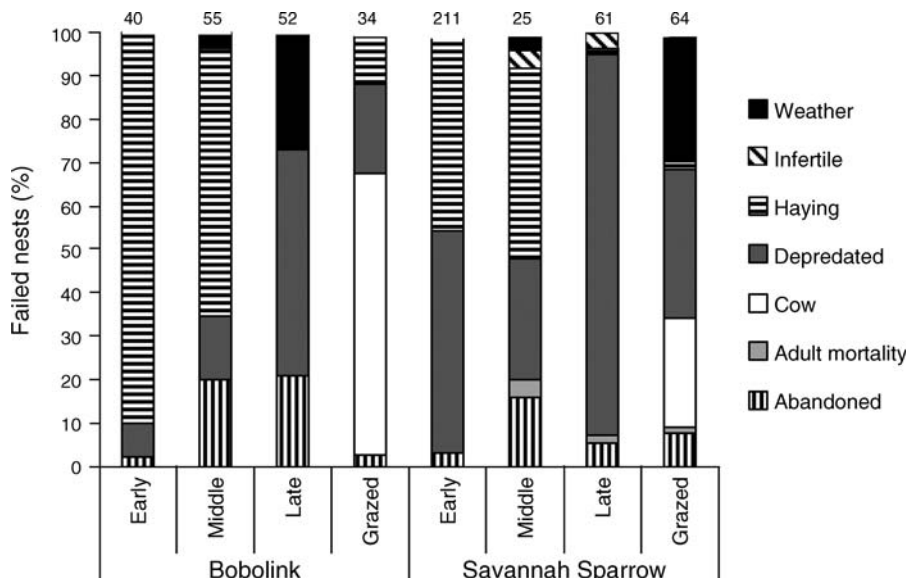


FIG. 3. Causes of failure for all failed Savannah Sparrow and Bobolink nests in the Champlain Valley (New York and Vermont) 2002–2005 (sample sizes are above bars). Types of failures were generally associated with treatment type. Note that failure due to haying includes nest loss during hay harvest and secondary losses due to predation or abandonment.

Nest success and daily nest survival

Grassland management was the strongest factor affecting nest success and daily nest survival (Table 2). All models that received weight of support >0.01 included field treatment as a variable. The treatment × species interaction model ranked highest ($\omega_i = 0.57$), with 2.1 times more weight of support than the next-best-ranking model. Models of lower rank and weight illustrated that year and species effects were also important. The treatment-only model received an AIC_c weight of only 0.03, which further suggested that treatment alone did not affect nest survival.

The coefficients within our L-E linear models indicate the strength and direction of the effect for each of the model factors relative to the reference factor (Appendix A).

The early-hayed treatment had the greatest negative effect on nest success of the four treatment types, with coefficients ranging from -0.99 to -1.75 across the six highest ranking models (Fig. 4a, b). Grazing had the second strongest negative effect. We have high confidence in the biological relevance of these effects because only one of the confidence intervals for the 12 coefficients (ranging from -0.35 to -0.70) for early-hayed and grazed treatments overlapped 0, and that estimate overlapped 0 by a marginal amount (grazed: treatment × year: 95% CI = -1.16 – 0.08). Our data suggested no biologically meaningful difference in daily nest survival between middle-hayed and late-hayed treatments (Fig. 5).

In the three ranking models that included species as a parameter, the coefficient estimates clearly indicated

TABLE 2. Logistic-exposure model set for nest success with corresponding ranking values for Savannah Sparrow and Bobolink nests in the Champlain Valley (New York and Vermont) 2002–2005.

Rank	Model	K	Deviance	AIC_c	Δ_i	ω_i
1	treatment × species interaction	8	4050.41	4066.43	0.00	0.57
2	treatment × year interaction	15	4037.82	4067.90	1.47	0.27
3	treatment + species + year	8	4055.20	4071.23	4.79	0.05
4	treatment + species	5	4061.80	4071.81	5.37	0.04
5	treatment + year	7	4057.97	4071.99	5.55	0.04
6	treatment	4	4064.36	4072.37	5.94	0.03
7	year × species interaction	8	4134.95	4150.98	84.54	0.00
8	year + species	5	4170.71	4180.72	114.29	0.00
9	year	4	4176.38	4184.39	117.95	0.00
10	species	2	4185.97	4189.97	123.53	0.00

Notes: K is the number of estimated parameters; DEVIANCE is the $-2(\log \text{likelihood})$; AIC_c is a second-order correction for AIC that is computed as $DEVIANCE - 2K$; Δ_i measures the difference in AIC_c between model i and the best-fitting model; ω_i is the AIC_c weight, interpreted as the probability of being the best model in the model set.

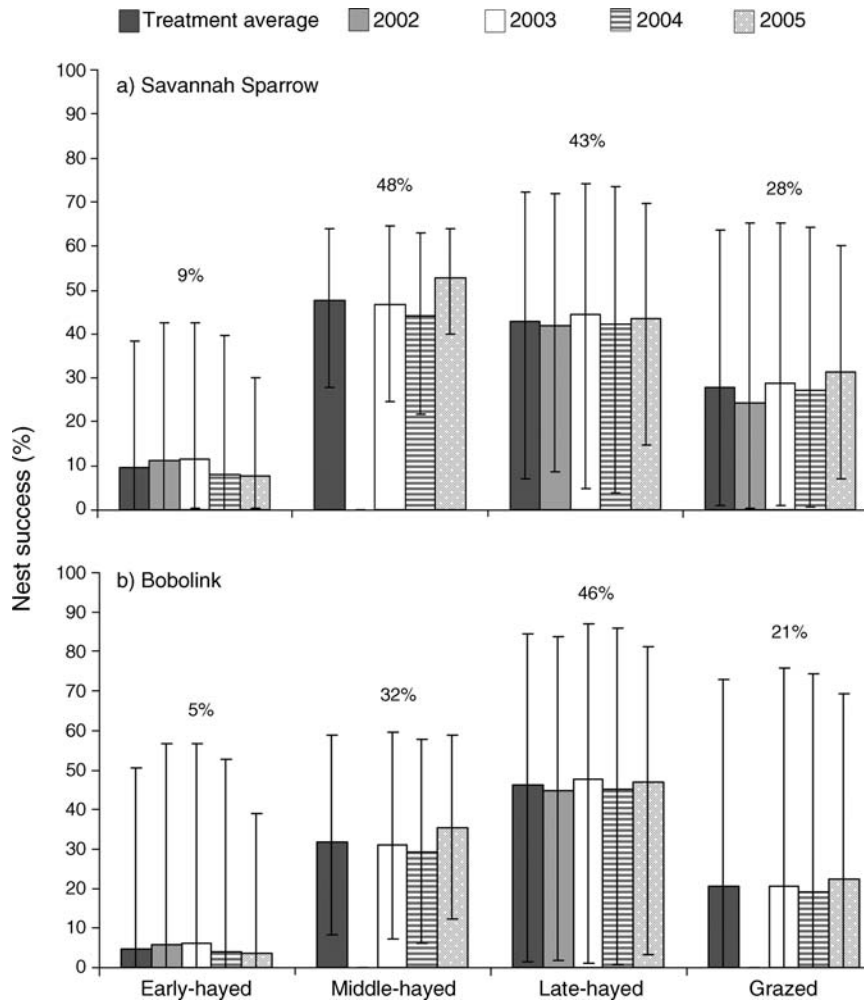


FIG. 4. (a) Savannah Sparrow and (b) Bobolink logistic-exposure model-averaged nest success (mean and 95% CI) in the Champlain Valley (New York and Vermont) 2002–2005. The numerical value for each treatment average is given above the histogram bars.

that the effect of the grassland treatment was stronger on Bobolinks than Savannah Sparrows (Appendix A). The Bobolink coefficients ranged from -0.17 to -0.63 . While two of three coefficients overlapped 0, we have high confidence in these estimates because the overlap was marginal (treatment + species: 95% CI = -0.37 – 0.04 ; treatment + species + year: 95% CI = -0.37 – 0.03).

Apparent nest success

While we believe that the logistic-exposure method is the most appropriate technique with which to analyze our data; model results are not comparable to studies that report either apparent nest success (ANS) or Mayfield-corrected (Mayfield 1975) nest success. Thus for comparative purposes, Appendix B reports apparent nest success, which was in nearly all cases noticeably different, and generally greater, than our L-E values for nest success.

Grassland management surveys

The Champlain Valley is a dynamic landscape with noticeable year to year variation in management, where the majority of available hayfield habitat was hayed at some time during the breeding season. Hayfields represented between 58% and 63% of all agricultural lands and 75–80% of all surveyed grasslands. Pastures accounted for 16–20% of all agricultural lands and 20–25% of all grasslands in the Valley. By 1–4 June, between 3% and 8% of hayfield habitat was cut; by 12–16 June, between 25–40% was cut; and by 28 June–2 July, 32–60% was cut (Fig. 6). In terms of our defined treatments, between 19% and 32% of hayfields were cut by the end of the early-hayed period (11 June); 27–49% of hayfields were cut by the beginning of the middle-hayed period (21 June); and 32–69% of hayfields were cut by the end of the middle-hayed period (10 July). Additionally, 59%

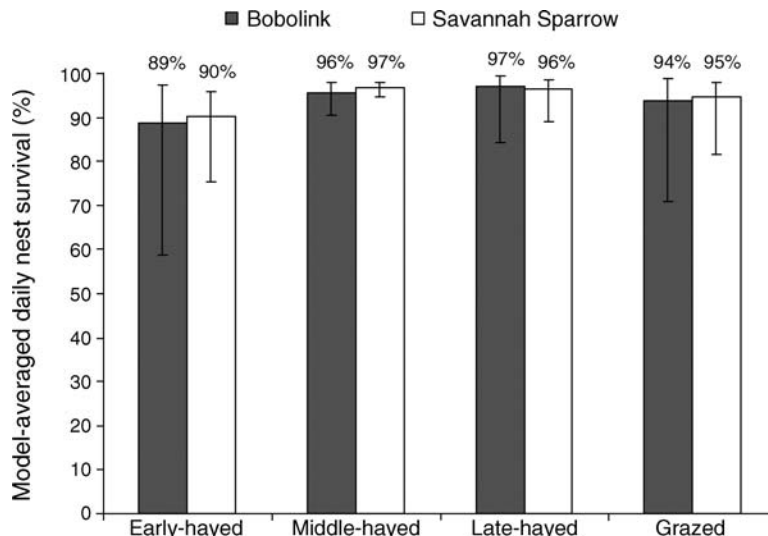


FIG. 5. Bobolink and Savannah Sparrow logistic-exposure model-averaged daily nest survival (mean and 95% ci) in the Champlain Valley (New York and Vermont) 2002–2005. The mean value for each species is given above the histogram bars.

of early-hayed habitat was hayed a second time during the breeding season.

DISCUSSION

Our results describe a gradient of demographic responses among four grassland habitats defined by management practices. For all response variables, early-hayed fields were low quality habitats for reproduction. Female Savannah Sparrows on middle- and late-hayed fields fledged 2.6–2.7 times more young each year than females on early-hayed fields, even though females on early-hayed fields built more nests and laid more eggs.

The effects of early haying on phenology and breeding success did vary, however, between species and among years. For female Savannah Sparrows, the number of annual fledglings produced was >1.0 on early-hayed fields because females remained on the fields and often re-nested immediately after haying. In fact, some females began laying eggs two days after haying in nests built in 10–12 cm of grass, but re-nesting patterns varied between years. When females were more immediate and synchronous in re-nesting after haying, they tended to fledge nests before a second cut in mid-July. In some years re-nesting was asynchronous, and nearly all nests failed

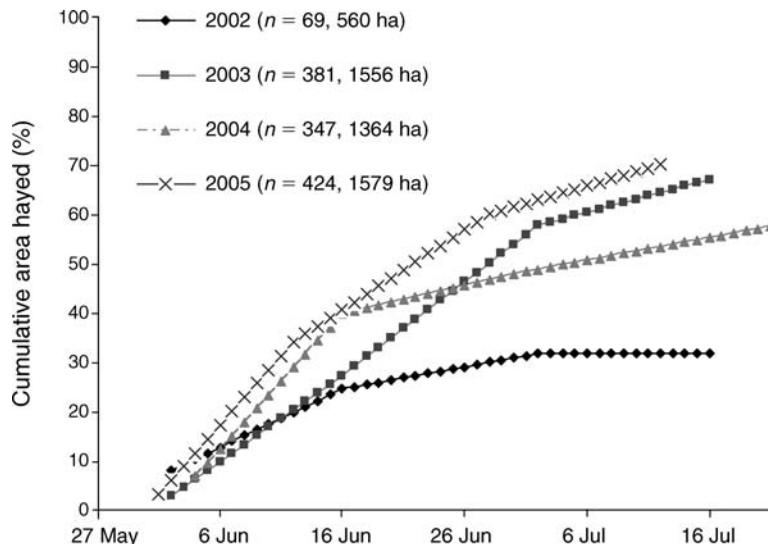


FIG. 6. Cumulative area hayed, Champlain Valley, Vermont, 2002–2005. By 1–4 June, between 3% and 8% of hayfield habitat was cut; by 12–16 June, between 25% and 40% of hayfield habitat was cut; and 32–60% was cut by 28 June–2 July. Additionally, 59% of hayfields cut before 11 June were cut a second time during the breeding season. We also report *n*, the number of fields surveyed during cutting.

with the second haying. When second hay cuts caused all nests to fail, some females remained on the field and re-nested again in late-July.

Predation rates between the first and second haying were highly variable. In extreme years, predation caused 59–69% of failures on early-hayed fields, while in other years only 9–18% of failed nests were depredated. High predation resulted in asynchronous re-nesting, which again caused more nests to be vulnerable to a second mid-July haying. This stochastic nature of predation resulted in some years in which the number of fledglings produced by female Savannah Sparrows on early-hayed fields was near 0 and others where the number of fledglings produced was near 2.0.

In contrast to Savannah Sparrows, the number of fledglings produced by female Bobolinks on early-hayed fields was near 0. Including nesting attempts before and after haying, only one Bobolink nest was successful on an early-hayed field. This nest was initiated after the first haying, where a female nested in a small, wet, uncut strip in the field. However, some Bobolinks may have emigrated and re-nested in other areas. These results are similar to Bollinger et al. (1990), where mid-June haying resulted in ~94% nest failure.

We are confident that we did not miss successful Bobolink nests on the early-hayed treatments because all Bobolinks abandoned the field within two days following a haying event. Additionally, our Bobolink sample for the first cut on the early-hayed fields underestimates the actual number of breeding females because many were still in settlement, nest building, and egg laying stages. Our field observations and banding records indicated that these females were committed to territories even though not yet identified with an active nest. Regardless of their breeding stage at the time of haying, no banded female returned to nest in an early-hayed field after the field was cut (some returned between years). Perhaps most important to management options, the timing of the first haying influenced the probability that Bobolinks would repopulate early-hayed fields. In all years, no Bobolinks were present during the first two weeks after haying. Only novice (unbanded) female Bobolinks repopulated fields cut before 2 June ($n = 3$) within the same year. This information suggests that early-hayed fields were sinks and most likely the post-cut breeders using them were recruited from other areas.

These nesting patterns contrast the behaviors observed by Bollinger et al. (1990). In their study, 24% (5 of 21) of female Bobolinks re-nested in unmowed sections of the field in which mowing caused nest failure. Like late-nesting females in this study, Bollinger et al.'s (1990) re-nests all failed due to subsequent haying. A critical difference between studies, though, is that only novice females repopulated fields hayed *prior to 2 June*, as early-hayed fields rarely have unmowed sections.

Middle-hayed fields offered high quality breeding habitat, similar to late-hayed fields. In fact, the number of fledglings produced by Savannah Sparrow females

was greater on middle-hayed fields than late-hayed fields (+0.18 fledglings/year, Table 1; +5% nest success, Fig. 4). This trend was not, however, true for Bobolinks (−0.57 fledglings/year, Table 1; −11% nest success, Fig. 4), although the number of fledglings produced was greater than female–female replacement and nest success was relatively high on middle-hayed fields. The relatively high levels of success for both species on middle-hayed fields is particularly surprising because it is contrary to the current hay–land conservation dogma in the Northeast, where fields cut during the breeding season are considered poor quality and conservation organizations advise landowners to delay hay harvest until at least 1 August (Massachusetts Audubon Society 2003, Natural Resources Conservation Service 2005).

Late-hayed fields have other values not observed on middle-hayed ones. Savannah Sparrow fledging took place over a 67-day and 64-day window on the middle- and late-hayed treatments, respectively. However, from 2 July to 17 July (15-day window), 0% of nests fledged on middle-hayed fields, while 26% of all nests fledged on late-hayed fields (Fig. 1). Lack of fledging during this window is a product of the nest failure caused by middle-haying dates and subsequent re-nesting cycles. As Savannah Sparrow re-nesting behavior between early-, middle-, and late-hayed fields was similar, they had the full 64-day window to nest on late-hayed fields, while they only had a 52-day window on middle-hayed fields. The longer window on late-hayed fields provided additional time for females to re-nest after predation or weather events, including females already on the field as well as immigrants from other fields whose nests had likely failed due to cutting.

This hypothesis can be inferred from Bobolink phenology and banding data. The first Bobolink nest fledged three days earlier on middle- than late-hayed fields. Bobolinks fledged during a 16-day window on middle-hayed and a 42-day window on late-hayed fields (Fig. 1). Integrating phenology data with the banding data showing that only “novice” Bobolinks repopulated very early-hayed fields, suggests that given appropriate habitat, Bobolinks will continue to build nests and lay eggs into late June. However, only 7% of successful and unsuccessful Bobolinks stayed and re-nested on late-hayed fields, evidence that most late-nesting females must be new to their respective fields. Therefore, the late nesting females on the late-hayed fields presumably settled initially in other habitats in which their first nests failed or they failed to gain a territory. It is unlikely that females failed to gain territories, however, because Bobolinks in Vermont generally have a polygynous social structure where males pair with multiple females (N. Perlut, *unpublished data*). Thus, most first nests of late or repopulating females must have failed due to weather, predation, or grassland management. In fact, 39% of all successful nests on late-hayed fields fledged after 29 June, the last date of observed fledging on middle-hayed fields. Thus, late-hayed fields can serve as

high-quality habitats for these late-nesting, displaced females.

Hayfield management is highly variable between years; however, the majority of hayfields were cut during the breeding season. As much as 32% and as little as 19% of hayfield habitat was mowed by 11 June, the end of the early-hayed period. Additionally, 59% of the early-hayed habitat was cut a second time within the breeding season. For comparison, Bollinger and Gavin (1992) observed similar cutting trends in central New York. Over a four year period, they observed between 10% and 30% of area harvested by 11 June, but somewhat greater areas harvested by mid-July (60–78% central New York; 32–69% Vermont). One noticeable difference between these data and Bollinger and Gavin (1992) is a greater annual variation in Vermont. Our demographic results within the context of the cutting survey help explain Savannah Sparrow (−0.17%/year) and Bobolink (−3.05%/year) population declines in Vermont (1966–2004; Sauer et al. 2005).

Comprising 20–25% of all grasslands in the Champlain Valley, pastures are important nesting habitats to consider within this agricultural landscape. Our research, however, should be interpreted cautiously, as these results may not apply to other (non-rotational) grazing regimes. Among the four treatments, nest success (28% Savannah Sparrow, 21% Bobolinks) was moderate on pastures and similar or higher than the Mayfield-corrected and apparent nest-success results of other natural and simulated nest-success studies (Jensen et al. 1990, Paine et al. 1996, Temple et al. 1999, Lapointe et al. 2000, Ignatiuk and Duncan 2001). Female responses to nest failure on pastures were similar to the three hayed habitats. Savannah Sparrows remained on the field and quickly re-nested. While most female Bobolinks did not re-nest, they were more likely to re-nest on pastures than any other treatment. The consistent timing of cow rotation created a mosaic of grass heights within a given farm. This diverse habitat likely caused more female Bobolinks to remain on the field and re-nest rather than to leave and search for suitable habitat elsewhere. This study may be the first to document annual, individual female breeding characteristics within rotationally grazed pastures, as we were unable to identify any comparable studies.

Management implication

The difference in the reproductive timing between these two species creates a complex community for land managers trying to balance birds' requirements for successful reproduction with farmers' resource demands. Our results strongly endorse the value of late- and middle-haying as management options that create "source" breeding grounds for Bobolinks and Savannah Sparrows. The question land managers face, however, is how to turn early-hayed fields into more stable habitats where females can, at a minimum, reproduce at replacement. Our data indicate that the key variable is

the timing of the second haying event. While Savannah Sparrows gained modest reproductive success on early-hayed fields, a 45-day window between 28 May and 12 July was insufficient for Bobolinks to fledge young. At the time of second haying, most nests were in the middle to late nestling stage. Wheelwright and Templeton (2003) estimated Savannah Sparrows require a minimum of 12 days for fledglings to acquire basic foraging skills. Therefore, given an additional 8 days to complete fledging and 12 days for fledglings to become sufficient foragers, we suggest cutting intervals of 65 days may be sufficient to support both Bobolink and Savannah Sparrow reproduction within an early-hayed system. However, if the first haying occurs after 2 June, the probability of Bobolink repopulation may be from low to zero. Therefore, for a 65-day window between first and second cuts to benefit both species, farmers should attempt to cut early-hayed fields as early as possible. The ability to delay the second cut will be a farm-by-farm decision, mainly determined by livestock nutritional needs. An initial May harvest will produce a moderate volume of high-quality, protein rich forage. A delayed second harvest will produce a comparatively lower protein-rich forage, though with a greater volume. This early-haying plan will therefore be most applicable to farms that house some combination of horses, heifers, beef cows, dry cows, or lactating dairy cows, which often have diverse nutritional needs. The timing of cuts on middle-hayed fields is critical to the potential reproductive success of Bobolinks. In this management option, farmers producing hay for horses have the greatest flexibility to conduct first cuts during this period. As both species show relatively strong fidelity to breeding sites (N. Perlut, *unpublished data*), interannual consistency in management practices is a critical factor in maintaining habitat quality over the long-term.

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APPENDIX A

Coefficient estimates and model structure description for logistic-exposure nest-success models (*Ecological Archives* A016-070-A1).

APPENDIX B

Comparison between logistic-exposure and apparent nest success, along with discussion and interpretation of the model of nest survival as a function of haying data (*Ecological Archives* A016-070-A2).